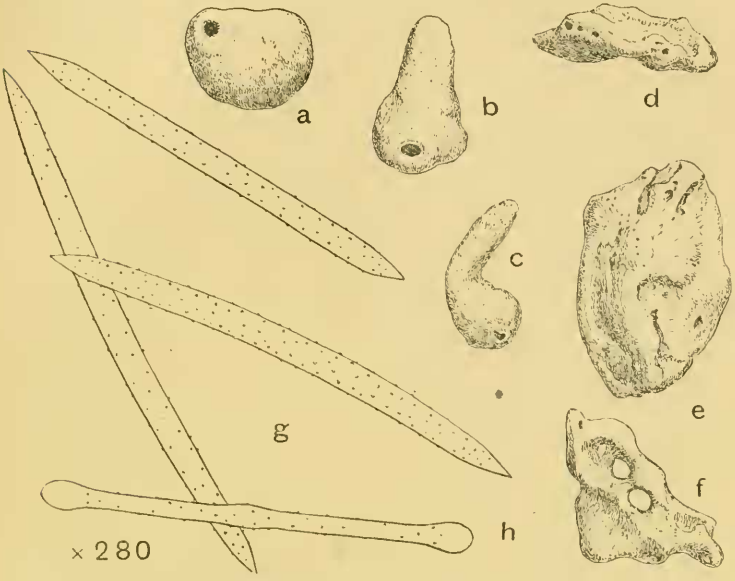
Two months later Mr. Hill sent a further consignment. Gemmules were now found, and the sponge was at once recognized as *Ephydatia kakahuensis*, Traxler (Termés. Füzetek. 1896, xix. p. 102, pl. ii.). The sponge described by Traxler came from the River Kakahu in the South Island.



Ephydatia kakahuensis, Traxler.

a–f, specimens $\frac{1}{2}$ natural size: **a**, **b**, **c**, conical, with one large oscule; **d**, lamellar; **e**, thinly encrusting; **f**, irregular; **g**, spined tornote oxeas, × 280; **h**, exceptional shape, viz. amphityle, × 280.

Accordingly, New Zealand continues to have only one known species of freshwater sponge, this being found both in the North and South Island.

It is to be hoped that Mr. Hill, who intends to dredge in Lake Taupo, will add to the number of species.

XXXIX.—*On the Anatomy and Affinities of* Hypsobia nosophora. By G. C. Robson, B.A.

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Introduction.

In 1915 Leiper and Atkinson (6), in extending and confirming Miyairi's original conclusions with regard to the transmission of Asiatic Schistosomiasis (=Bilharziasis),

announced that part of the life-cycle of *Schistosoma japonicum* was passed in the tissues of a Japanese freshwater snail. This snail was described by the present author (10) as *Katayama nosophora*, and a short account of the radula, shell, and operculum was given.

In May 1915 Pilsbry (9) referred this form to *Blanfordia*, and in 1918 Annandale (2) placed the species in Heude's *Hypsobia*. There can be little doubt that the mollusc in question should be referred to the genus described by Heude under that name.

As no complete account of the structure of this animal has apparently been published, and the descriptions of Heude and the present author were only slight and confined principally to external features, it has been thought desirable to issue some detailed account of its anatomy. In addition to its rôle as intermediate host to *Schistosoma japonicum* and as a member of a group of Mollusca the anatomy of which is very little known, the discovery by Cort (4) of its powers of resistance to dessication rendered the study of its respiratory system an inviting subject.

It is not the object of this paper to discuss the nomenclature of this group of Gastropoda, as the amount of information upon the structure of E. Asiatic *Paludestrina*-like molluscs is too scanty to justify a taxonomic discussion.

It is open to those interested in nomenclature to criticize Pilsbry's reference of this form to *Blanfordia* or to inquire whether Heude's genus should not be called *Blanfordia*; but, until we have a general knowledge of the structure of all the genera involved in this question, such discussions appear a little premature.

The publications of Bregenzer (3), Seibold (13), and the present author (11, 12) serve to show that there are several characters of fundamental importance which cannot be neglected in the classification of the *Paludestrina*-forms ; and it is very much to be regretted that in his admirable survey of the freshwater Hydrobiidæ of India (1) Dr. Annandale should have ignored such characters as the nervous system and female genitalia.

The author is indebted to Dr. W. W. Cort, of the Johns Hopkins University, for sending living examples of the snail and for information concerning its mode of life.

Structure.

I. *Alimentary System.*

The general disposition of the *mouth* and its adjacent area

resembles that found in the Paludestrinidæ. The mandibles, the epithelium which secretes the oral cuticle, and the two lateral diverticula of the mouth are in general like those of *Paludestrina jenkinsi* (11) or *ventrosa* (12). The mandibles consist of seventeen to twenty-one columnar pieces of specialized cuticle.

The secretory epithelium is continuous with that of the pharynx.

Posteriorly to the mandibles the mouth widens out and is flattened over the oral cartilages. It shows the tripartite arrangement seen in other Paludestrinids. The median portion has a thin non-ciliated roof, and the lateral portions dip down beside the cartilages.

The *salivary glands*, of which there is a single pair, open into the lateral divisions just behind the level of the radula and cartilages. They come into intimate connection with each other across the œsophagus ; but it is doubtful whether actual organic fusion occurs.

The *buccal cartilages* are symmetrical and joined in the median line. Laterally they are somewhat flanged upwards, while posteriorly they are divergent.

The *radula* has been described elsewhere (10), while that of *H. humida* was figured by Heude (5). In the material forwarded by Dr. Cort there was a tendency for the animals to show one less denticulation on the two outer teeth than is shown in the original description of *H. nosophora*.

The *stomach* corresponds in its general structure with that of other Paludestrinidæ, though the apertures of the œsophagus and hepato-pancreas are not so close together as in *Paludestrina*. The point of entrance of the œsophagus was rather variable in the individuals examined. The cuticular lining, the marked transverse ridge of the upper portion of the stomach, and the position and structure of the *style-sac* are remarkably similar to the condition seen in *Paludestrina*. The communication between the pylorus and style-sac characteristic of the latter genus is also found in *Hypsobia*. The layer of dark pigment-granules in the stomach epithelium of *Paludestrina* and *Bythinella* (3, 12) was not found in this genus, though its absence may be due to accidental causes.

The *intestine* exhibits a typhlosole. The rest of the alimentary and digestive system does not call for special comment.

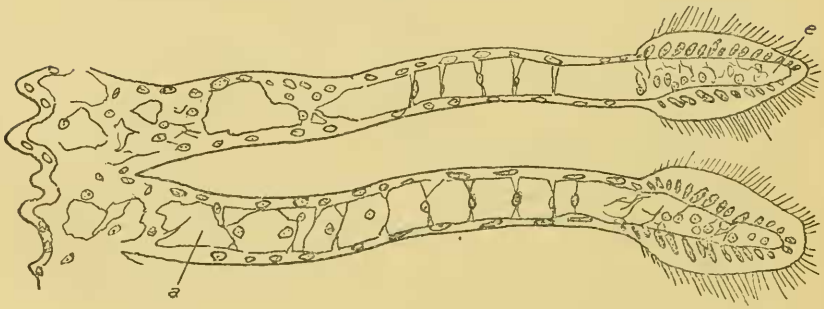
II. *The Respiratory System.*

The character of the *gill* constitutes the most remarkable feature in the structure of this animal, and differentiates

Hypsobia at once from *Paludestrina* in this respect. The author is not inclined, however, to regard it as of very great taxonomic importance. The points of agreement between the two genera are so numerous that the specialized nature of the respiratory apparatus in *Hypsobia* may, on the whole, be disregarded for classificatory purposes.

As in *Littorina* (8) and *Hemibia* (5), the filaments of the gill are prolonged across the roof of the mantle-cavity to the rectal border. This modification of the gill has been very fully discussed by Pelseneer (*loc. cit.*) ; and according to his description the condition seen in *Hypsobia* and *Hemibia* is comparable exactly to the stage illustrated by *Littorina*, in which each filament is reduced in height and continued right across the pallial cavity, but has not yet broken up into the vascular arborizations seen in *Cerithidea*.

Fig. 1.



H. nosophora ($\frac{1}{12}$ hom. imm. × 4 oc.).

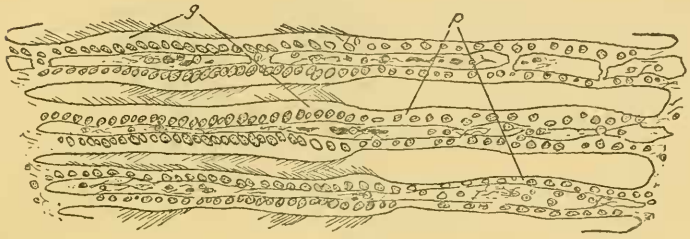
Section through two gill-lamellæ. *a*, afferent vessel ; *e*, efferent vessel.

I propose to refer to the " filaments " or " lamellæ " of the true gill, and to call the ridges by which they are continued " paractenidial " folds or filaments. There are from forty-eight to fifty-four lamellæ. Each of these in side-view appears as an oblong, slightly bent plate tapering to a blunt point at the right-hand end. This end is actually free, though supported by the paractenidial filaments. The vascular system of each filament consists, as usual, of dorsal afferent and ventral efferent vessels, with an intermediary system of lacunæ (fig. 1). In general, the condition seen resembles that in *Bythinella dunkeri* (3) and *P. ventrosa* (12), though the walls are much thicker and the spaces more

confined than in those forms. The paractenidial folds differ from the above in having no expanded ciliated portion. Otherwise they do not differ from the true gill. The lacunar system is continuous from the filaments into the paractenidial folds (fig. 2).

The afferent vessels are derivatives of an irregular lacunar system communicating with the ample rectal sinus.

Fig. 2.



H. nosophora.

Horizontal section through base of gill-lamellæ (*g*) and paractenidial filaments (*p*).

All that is known of the habits of this animal points to its being amphibious. Heude says of the Chinese species that it does not live in water, but on damp rocks. No such details of the actual mode of life of the Japanese species are available; but Cort (4) has shown that it will leave the water voluntarily and can resist dessication for about three months.

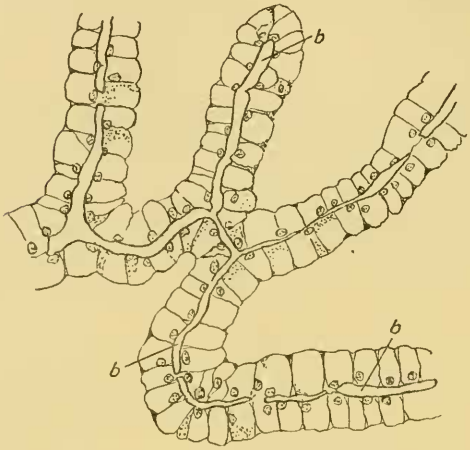
III. *Renal System.*

The *kidney* is rather remarkable among the *Paludestrina*-like forms on account of its complexity. In all the specimens examined it was possible to distinguish three areas, which were, however, by no means constant in their distribution or histological condition.

1. *Trabecular Portion.*—This consists of a number of cavities separated by a trabecular system covered by the same type of epithelium as the open portion of the kidney. In the walls of these cavities are found numerous blood-spaces (fig. 3).
2. The "*blood-gland*" is a compact stroma usually lying near the renal aperture at the anterior end and on the outer side of the kidney next to the body-wall.

3. The *urinary cavity* ("Urinkammer") resembles that found in the Paludestrinidæ. It ramifies among the other organs, and is lined by a characteristic epithelium composed of vacuolated cells with basal nuclei.

Fig. 3.



H. nosophora ($\frac{1}{12}$ hom. imm. × $\frac{1}{4}$ oc.).

Part of trabecular area of kidney. *b* = blood-spaces.

IV. *Circulatory System.*

The *pericardium* is situated in the usual position. No trace of a reno-pericardial aperture was found, though it is not certain that it is absent.

The *auricle* and *ventricle* are normal. The latter is very muscular and its cavity is traversed by numerous muscle-fibres. Some indication is seen of an auriculo-ventricular valve.

The distribution of anterior and posterior aortæ is normal, the anterior running forwards over the roof of the pericardium for some distance, then accompanying the œsophagus to open into the cephalo-pedal sinus. The posterior aorta runs backwards between the stomach and intestine. It would appear that the portal vein enters the pulmonary vein before the latter reaches the auricle; but it is impossible to be absolutely certain of this point.

The cephalic and pedal portions of the *anterior* (*cephalo-pedal*) *sinus* are incompletely separated by a horizontal

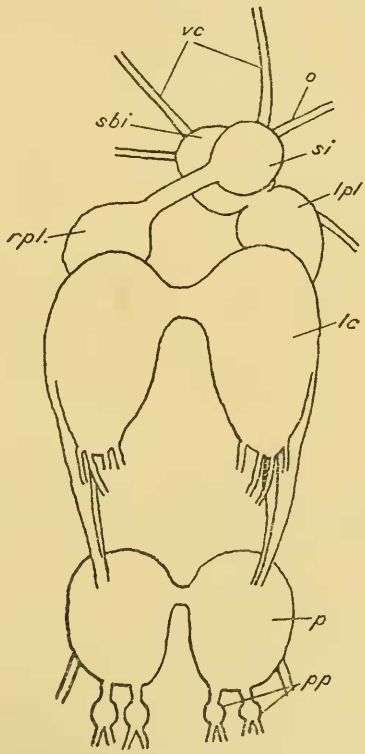
septum [*cf.* Robson (12)], which, as in the Paludestrinidæ, passes between the pedal ganglia and the cerebro-pleural complex.

V. *The Nervous System.* (Figs. 4 & 5.)

(a) *Sense-organs.*

1. *Osphradium.*—This is a small rod-shaped organ lying, as usual, on the left-hand side of the gill. It is innervated by a conspicuous nerve rising from the supra-intestinal ganglion.

Fig. 4.



H. nosophora. Central nervous system (anterior aspect).

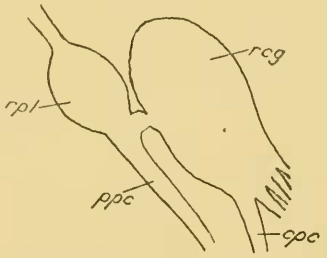
lc=left cerebral ganglion; *lpl*=left pleural ganglion; *p*=pedal ganglion; *rpl*=right pleural ganglion; *pp*=(sc.) parapodial and propodial ganglia; *si*=supraintestinal ganglion; *sbi*=subintestinal ganglion; *o*=osphradial nerve; *vc*=visceral commissure.

2. *Otocysts.*—These are found in the usual position on the posterior surface of the pedal ganglia. They contain a single otolith. The auditory nerve is very difficult to follow, and is apparently fused with the cerebro-pedal connective.
3. *Eyes.*—These are situated at the base of the tentacles and on the outer side. They consist of inner and outer cornea, a well-developed lens, and retinal layer.

(b) *Ganglia and Nerves.*

The cerebral ganglia are elongate and rather pointed anteriorly. They are placed with their long axes parallel to the main axis of the pharynx. They are connected in the median line by a small commissure. The pleural ganglia are closely applied to the cerebral ganglia, but are not fused to the latter. There are very short but distinct cerebro-pleural connectives [*cf.* discussion upon the latter in *Paludestrina ulvæ,* Robson (12)].

Fig. 5.



H. nosophora. Cerebro-pleural connective.

rpl=right pleural ganglion ; *rcg*=right cerebral ganglion ; *ppc* and *cpc*=pleural-pedal and cerebro-pedal connectives.

The cerebro-pedal and pleuro-pedal connectives are distinct, though very closely applied to each other. The pedal ganglia are rather round. They are closely approximated, being joined by a small commissure.

The supra-intestinal ganglion is joined to the right pleural ganglion by a commissure slightly longer than that figured by Bregenzer for *Bythinella dunkeri* (3). From this ganglion are given off the osphradial nerve and a connective to the abdominal ganglion.

The subintestinal ganglion is very closely approximated to the left pleural ganglion, but not fused to it.

The abdominal ganglion is situated between the anterior end of the kidney and the columellar muscle.

The cerebral ganglia give off anteriorly ocular, tentacular, and labial nerves, and connectives to the buccal ganglia.

It would appear that the penis-nerve is of cerebral origin, though it is impossible to make absolutely certain of this. It is possible that the tentacular nerve supplies branches to the musculature of the eye.

Each of the pedal ganglia gives off three main nerves, the two anterior ones bearing small ganglia at a short distance from their roots. These ganglia in their turn give off each two nerves which apparently innervate the plantar musculature of the foot.

VI. *Reproductive System.*

Male Organs.

The *spermatozoa* have long and tapering heads, differing therein from those of *Paludestrina* (12) and *Bythinella* (3), and agreeing rather with *P. taylori* (sc.=*Amnicola*) (Robson MS.). Whether they possess the extraordinarily long tail seen in the latter is, however, doubtful.

The *vas deferens*, after quitting the region of the testis, becomes progressively more slender. It passes into the *prostate*, which is of considerable size, and on quitting the latter it passes over the floor of the mantle-cavity and up the penis surrounded by a thick layer of circular muscle.

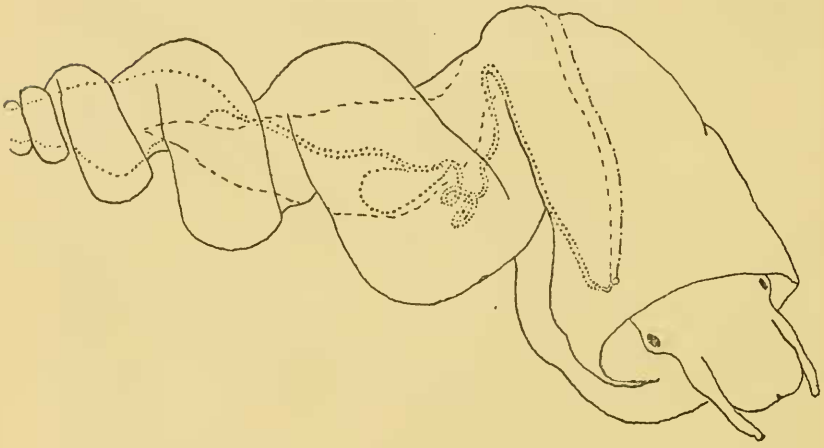
The *prostate* is very much folded. The cells lining its cavity are sparsely ciliated. It is difficult to be very certain about the histological elements composing this gland. In the first place, it usually showed differential staining, certain areas being more darkly stained than others. But it is impossible to say whether this was due to the presence of different types of cells or different physiological states of a single type of cell. It was possible to distinguish (*a*) vacuolated cells with the nucleus somewhat flattened out and found very often at the interior end of the cell (the end next the lumen of the gland), and (*b*) cells with eosinophilous granular cytoplasm, with the nucleus more usually rounded and occupying a more median position.

The penis is undivided, agreeing therefore with *Paludestrina*, *Hemibia*, *Delavaya*, *Stenothyra*, and *Tricula*, and differing from the Bythiniinæ (1). It is cephalic in position. In all the examples dissected it was rather broader and stouter than that figured for *H. humida* by Heude (5).

Female Organs. (Figs. 6 & 7.)

The *oviduct* follows the usual course downwards from the ovary. In the neighbourhood of the stomach it gives off a spermatheca of a rudely ovoid shape. The oviduct then becomes convoluted as in *P. ventrosa,* straightens itself out again, and runs parallel to the "uterus" and its glandular annexe along the right-hand side of the pallial cavity external to the "uterus." It terminates in a small aperture adjacent to the uterine aperture and anus. The lower end of the oviduct is very slender and its aperture exceedingly

Fig. 6.



H. nosophora, × 22. Female reproductive system.

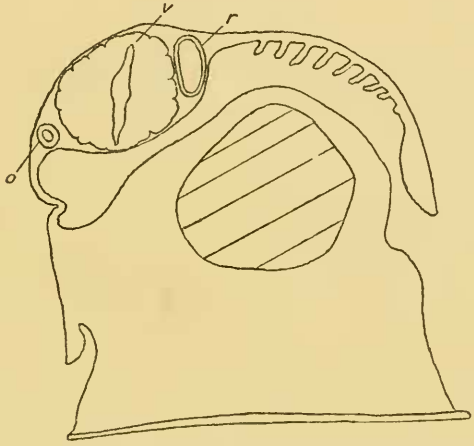
.....=ovary, oviduct, and spermatheca; – – – – –=accessory gland and uterus; – . – . – . – .=rectum.

small, and it is very difficult to see how intromission is effected. Fertilization is internal, however, as spermatozoa may be frequently found in the spermatheca. It is similarly difficult to imagine how the fertilized ova find their way into the uterus, as they must first be shed into the pallial cavity and then be drawn into the uterus. The problem is the same in such forms as *Melania* and *Tanganyikia* (Moore, 7), in which a groove connects the oviducal aperture with the brood-pouch.

The author was at one time inclined to think that a connection existed in *Hypsobia* between the upper portion of the "uterus" and the oviduct in the neighbourhood of the receptaculum. But the connection between the two organs at this upper level, which was found in one or two examples only, appeared to be fortuitous, and, in any case, there was no continuous passage from the cavity of the oviduct into that of the "uterus."

Arising at a high level (occasionally adjacent to the lower end of the ovary) an extensive gland is found which passes downwards and eventually appears as an elongate mass on

Fig. 7.



H. nosophora (×4 oc. × 6 obj.). Diagrammatic transverse section through median region of pallial cavity.

o = oviduct; *r* = rectum; *v* = "uterus."

the right-hand side of the last whorl. It has a continuous cavity throughout the whole of its length, which opens to the exterior close to the anus and oviducal pore in the anterior right-hand corner of the mantle-cavity.

It is impossible to discuss the identity and function of this gland without appropriately fixed material. It is evident, however, that it is divisible into two parts—an upper, wholly glandular portion, and a lower portion, less glandular, with a more capacious lumen and the remarkable feature of a well-developed muscular sheath imbedded in the glandular tissue.

The upper part usually stains a light blue with hæmatoxylin' the lower part an intensely dark bluish purple.

The author is inclined to regard the lower portion as a uterus * or brood-pouch. Although it is thick-walled and no eggs have been found in it, its lower portion in its position and relationship to the rest of the reproductive system resembles organs adapted for the reception and nutrition of the young, such as are found in neighbouring groups.

The *spermatheca* has a thick investment of circular muscle, and is usually composed of elongate secretory cells with basal nuclei. Spermatozoa were found in numerous examples, sometimes scattered throughout the cavity, sometimes clustered round the sides with their heads towards the periphery.

Affinities.

Along with *Hypsobia* Heude gave incomplete descriptions of several new genera, such as *Delavaya*, *Hemibia*, and *Fenouilia*, some of which show certain points of resemblance to *Hypsobia*.

We have only a very slight knowledge of the structure of the other Asiatic *Paludestrina*-like forms. The information as to the European forms is a little more complete. It must, therefore, be admitted that these resources are scarcely adequate to enable us to form a clear concept either of the natural groups into which the Paludestrinidæ (Hydrobiidæ, auct.) may be divided or of the limits of the family itself †. Admitting, then, that the family may be rather indefinite in its boundaries, it nevertheless cannot be doubted that the characters of the alimentary canal (including mandibles, cartilages, and radula), nervous system, and genitalia at once assign *Hypsobia* to the Paludestrinidæ. In what subfamily it should be placed is rather more uncertain. Some of its characters suggest that it should take its place very near *Paludestrina* itself, and at least in the same subfamily (radula, mandibles, style-sac, nervous system, and male genitalia). On the other hand, the specialized respiratory system, the kidney, the female genitalia, and the character of the spermatozoa do not seem to warrant its inclusion in the Paludestrininæ. Yet among the adjacent subfamilies—Bythiniinæ, Mysorellinæ, &c.—there is none in which it might be

* The upper portion may be an albumen- or a shell-gland, but for the time being the author prefers to call it the "accessory gland."

† The writer has had no opportunity of consulting Mr. B. Walker's "Synopsis of the Classification of the Freshwater Mollusca of North America," Mus. Zool. Michigan University, Misc. Publ. 6, 1918, p. 1.

placed with any confidence. If Heude's figure of the nervous system is to be trusted, *Hemibia*—with which *Hypsobia* shows such remarkable likeness in its specialized respiratory system—differs from *Hypsobia* in this respect as well as in the shell.

It would seem better to regard *Hypsobia* as the representative of a subfamily distinct from the Paludestrininæ, but approximating to them more closely than to other subfamilies the structure of which is known to us.

Conclusions.

(1) *Hypsobia* is a genus referable to the Paludestrinidæ, but probably representing a separate subfamily.

(2) It agrees with *Hemibia* and *Littorina* in showing an adaptation to an amphibious mode of life in the structure of its gill and pallial cavity, which is in accordance with what is known of its habits.

(3) It possesses a crystalline style-sac exactly comparable to that of *Bythinella* and *Paludestrina*.

(4) The female generative organs are peculiar in two respects—the large accessory gland with (sc.) uterine termination opening separately from the oviduct, and possibly comparable to the brood-pouch of other forms, and the muscular sheath imbedded in the glandular tissue of the latter.

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Note.—Miyairi's original paper, with the first reference (without description) to this mollusc, and Iwakawa's paper on the nomenclature and hibernation (Zool. Record, 1918) were not available for reference.